

Seed Banks in Soils

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I. INTRODUCTION

The term "seed bank" is a short and convenient one which has been widely adopted in recent years to denote the reserves of viable seeds present in the soil and on its surface. "Seeds" is used here in the broad sense to include fruits as well as true seeds, but not spores or propagules which are produced vegetatively.

Although Darwin (1859) took samples of pond mud and remarked upon the large numbers of seedlings that arose from seeds present in it, the first detailed study of seeds in the soil appears to be that of Putensen (1882) who examined their occurrence at three depths. Another early investigation was that by Peter (1893) who determined the seeds present in soil samples from forests. He showed that while only seeds of woody species occurred in ancient forests, those of species characteristic of arable fields or grassland could be found in the soil

beneath forests of more recent origin, and he concluded that many seeds could remain viable in the soil for more than 50 years. In the early years of this century, examinations both of seed populations in soils and of the techniques for quantifying them were made by workers in various countries (Mal'tsev, 1909; Snell, 1912; Wehsarg, 1912; Brenchley, 1918). Subsequently, detailed studies have been made in a range of vegetation types. Much of the information obtained about seed banks of grasslands has been reviewed by Major and Pyott (1966), who stressed the importance of considering the buried seeds as part of the flora. The investigations of seed banks of arable fields have been discussed by Kropáč (1966) and Roberts (1970). In comparison with the extensive literature on plant communities, however, that dealing with seed banks is relatively sparse, and it is only recently that much attention has been devoted to their role in "natural" habitats as distinct from those of agricultural importance.

The size of the seed bank, the relative contributions made to it by different species and the pattern of seed distribution reflect the seed production in the plant community and its surroundings not only in the preceding year but perhaps in many previous years. Seed banks are therefore of interest in the study of recent vegetational history, although the floristic representation is biased because of the considerable differences among species in seed output, dispersal and survival (Harper, 1977). The period for which seeds remain in or on the soil is also one of the phases which needs to be quantified in studies of the population dynamics of individual species (Sagar and Mortimer, 1976). For the applied biologist in particular, however, the aspect of greatest significance is the role of the seed bank in determining the future vegetation, especially after natural or deliberate perturbation.

In this article the techniques for studying seed populations in soils are considered first, since they have a bearing on the validity of the conclusions which can be drawn from investigations of seed banks. Its main purpose, however, is to review recent literature on seed banks in different vegetation types, with emphasis on the practical significance of the findings.

II. ESTIMATION OF SEED BANKS

The most direct method of detecting the presence of viable seeds in soil is to observe the emergence of seedlings *in situ*. If the existing vegetation is removed and the underlying soil is disturbed, the seeds present may be released from enforced dormancy (Harper, 1957) and innate or induced dormancy overcome because of exposure to light

(Wesson and Wareing, 1967) or to enhanced fluctuations of temperature (Thompson *et al.*, 1977). This method of estimation has been used in studies of seeds beneath steppe and forest vegetation (Korneva, 1970; Petrov, 1977), of long-term seed survival in undisturbed ruderal sites (Ødum, 1978) and of the establishment of *Trifolium subterraneum* from seed reserves (Beale, 1974). If influx of fresh seeds is prevented, the technique is positive in that all seedlings must have arisen from viable seeds. It is likely, however, that the germination requirements of many of the seeds present will not be met during the period of observation. So that although this method can be useful in certain circumstances, and can provide a measure of the seeds which are "available" at the time of soil disturbance, it does not provide a full statement of the seed bank.

The technique much more generally employed is to take representative soil samples and to determine seed numbers either by placing the soil under conditions suitable for germination, or by using physical methods of separation from the soil particles based on differences in size and/or density.

A. SAMPLING

The most usual requirement is for an assessment of the numbers of viable seeds of each species present in the soil of a defined area such as a plot or a field. The results are normally expressed as mean numbers of seeds m^{-2} and related to a soil layer of specified depth. The problems in sampling fields for dormant seeds are similar to those encountered in work with other organisms such as nematodes (Southey, 1970). There are errors associated with heterogeneity, which may occur on more than one scale. In the absence of prior information on distribution and when an average assessment over an area is required the arrangement of sampling points in a "W" configuration, as recommended for sampling soil for chemical analysis (Jackson, 1958) or sampling clustered plant-disease distributions (Lin *et al.*, 1979), seems likely to be satisfactory. If the aim is to determine changes in the seed bank along a gradient, for example in topography or distance from seed-bearing plants, then a transect approach would be appropriate.

For determinations of the surface seed bank, the seeds can be retrieved by suction from a delineated sample area. Samples of soil to a specified depth can be obtained by removing blocks of soil of known dimensions or by using a sampling tool which extracts a soil core perhaps no more than 2·5 cm in diameter. Provided that the design of the corer minimizes compaction, the cores can be sectioned to obtain samples from different

depths. Clay soils, however, are often difficult to sample by means of corers.

Studies of the sampling intensity necessary to estimate seed populations with prescribed degrees of accuracy in grassland (Rabotnov, 1958) and in arable soil (Smirnov and Kurdyukov, 1965) show that large numbers of samples are needed in order to obtain satisfactory results for individual species. Much depends on the seed density and distribution in the particular community under consideration, and most workers have compromised by taking what appeared to be a "reasonable" number of samples. As a general principle it seems wise to take a large number of small samples rather than a small number of large ones (Kropáč, 1966; Roberts, 1970; Dospekhov and Chekryzhov, 1972). Ideally a preliminary sampling study would be made, and even where this is not feasible it is desirable to obtain sufficient data to calculate whether increasing the sampling intensity would bring about a worthwhile gain in accuracy (Jones and Bunch, 1977).

One approach adopted in Japan has been to combine the sampling units to construct a species-soil volume curve in order to derive a minimum volume which will detect most species present. Minimum volumes found were 400 cm³ in the early stages of a succession (Numata *et al.*, 1964), 500–600 cm³ in grassland (Hayashi and Numata, 1971) and 4000–6000 cm³ in climax forest (Hayashi and Numata, 1968). Hayashi (1975) recommends that sufficient samples should be taken to make up twice the minimum volume.

Whipple (1978) tabulated the numbers and sizes of samples used in published studies of seed banks of non-agricultural communities in North America and concluded that because of the small surface areas they represented, the results should be viewed as estimates of the presence of species rather than of seed densities. Nevertheless, provided that the limitations are recognized, useful and valid results can be obtained, and if data are recorded separately for individual sampling units or replicated groups of them, estimates of error can be assigned to the mean values (Moore and Wein, 1977; Takahashi and Hayashi, 1978; Archibald, 1979).

The depth to which samples must be taken depends on the type of vegetation and the purpose of the investigation. In arable fields it may be sufficient to obtain an overall estimate of seed numbers in the cultivated soil layer, to a depth of perhaps 15 or 25 cm. Often, however, the occurrence of seeds in successive 5- or 10-cm layers is recorded (Kropáč, 1966; Fekete, 1975). Such data are necessary to evaluate the effects of different cultivation techniques on the numbers of seeds in the soil (Kazantseva and Tuganaev, 1972; Fay and Olson, 1978).

Some experiments have been done in which seeds of different kinds have been sown on the soil surface and their distribution in depth determined after various cultivations (Soriano *et al.*, 1968; Pawłowski and Malicki, 1969). In relatively undisturbed habitats, most seeds are usually found near the soil surface and for many purposes samples to a depth no greater than 5 cm may be adequate (van Altena and Minderhoud, 1972; Jones and Bunch, 1977). The depths at which concentrations of seeds of particular species occur may be significant in interpreting seed origin and vegetation history; sampling successive depth increments can provide data of this kind (Komendar *et al.*, 1973; Howard, 1974). Some detailed studies have been made in which both horizontal and vertical distributions of seeds in the soil have been determined (Želev, 1965; Kellman, 1978; Symonides, 1978).

The time of sampling in relation to the annual vegetation cycle must also be considered. In studies of the "survey" type, samples are often taken on a single occasion only, but although useful comparative data for different fields or localities can be obtained in this way, the results can be influenced by recent major inputs of seeds of particular species. Samples taken at the same time in successive years, however, can provide valid assessments of quantitative changes in the seed bank (Warington, 1958; Roberts and Dawkins, 1967; Barralis, 1972). To detect the changes that occur within the annual cycle, more frequent sampling is necessary. Recent studies of this kind have been made in a variety of plant communities including forest in Mexico (Guevara and Gómez-Pompa, 1972), sagebrush in Nevada (Young and Evans, 1975), psammophytes in Poland (Symonides, 1978) and for *Sporobolus airoides* in New Mexico (Knipe and Springfield, 1972).

B. SEEDLING EMERGENCE

In this method of determining the numbers of seeds in a sample, the soil is placed directly into a shallow container or spread in a thin layer on a suitable medium, kept moist, and the seedlings that emerge are identified and recorded. The aim is to ensure that as many as possible of the viable seeds present germinate and produce seedlings. If the soil contains a great deal of clay, its removal by washing through a fine sieve not only reduces the bulk but is likely to improve germination (Brenchley and Warington, 1930; Kropáč, 1966).

If only a single species is being studied, the samples can be kept under those conditions known to promote maximum germination of that particular species. Seeds of some species may require special procedures to overcome dormancy; Gratkowski (1964) obtained germination

of *Ceanothus velutinus* by first heating and then chilling the soil. Usually, however, a range of species is involved which differ in their requirements for germination. If the samples are kept for only a short period, and particularly if the conditions remain fairly constant, a biased estimate of the seed bank will be obtained. This may itself be of interest in providing a measure of the "available" flora at a particular time (Barralis, 1972; Young and Evans, 1975). Results reported by Mott (1972) give a striking illustration of the effects of temperature. When soil samples from an arid annual pasture were kept under diurnal fluctuations of 30/25°C seedlings of monocotyledons predominated, whereas at 20/15°C those of dicotyledons were more numerous. Other workers have subjected soil samples to a range of treatments in order to assess the effects of management practices on the resulting flora (Strickler and Edgerton, 1976; Howard and Smith, 1979). The time of year at which the samples are taken can also have a marked effect; those taken after the seeds have been exposed to natural chilling during winter may yield appreciably more seedlings than samples taken in autumn (Raynal and Bazzaz, 1973; Leck and Graveline, 1979).

Germination and seedling emergence are favoured if the soil layer is shallow and if it is periodically disturbed. Fluctuating temperatures promote germination of seeds of many species, and exposure to periods of low temperature or desiccation may be given to overcome dormancy (Barralis, 1972; Hurle, 1974; Johnson, 1975). Many workers have noted that seedlings of some species appear rapidly while others continue to produce seedlings over a long period. The samples must therefore be kept for a considerable time if a valid estimate of all viable seeds present is to be obtained. Vega and Sierra (1970) kept samples of a tropical soil for three years and found that 83% of all seedlings appeared in the first year, 16% in the second and 1% in the third. This is consistent with earlier results for arable seed populations in temperate countries, suggesting that a period of two years would be a reasonable compromise.

Vanesse (1976) reported that preliminary drying improved seedling emergence from samples of forest soil but Feast and Roberts (1973) found that while drying promoted germination of *Chenopodium album*, the numbers of seedlings of other annual weeds were either not affected or were depressed. None of the simple treatments which they tried gave any consistent improvement over their standard procedure in which the samples were exposed to diurnally and seasonally fluctuating temperatures in an unheated glasshouse. Germination of many aquatic species is affected by whether the substrate is covered by water or not,

and in studies of seed banks of wetlands it may be necessary to provide both these conditions (van der Valk and Davis, 1978; Leck and Graveline, 1979).

C. SEPARATION BY PHYSICAL METHODS

The second widely used method of enumerating seeds in soil samples utilizes differences in size or density to separate them from the soil components, although usually this is not entirely effective and hand-sorting is also required. Some published procedures are summarized in Table I.

1. Sieving

This entails washing the soil samples on sieves of appropriate mesh or pore size to reduce the volume of soil from which the seeds must be removed. In studies of individual species, sieving may be largely satisfactory by itself. With large seeds such as those of *Avena fatua* (Wilson, 1972; Wilson and Cussans, 1975) or *Ulex europaeus* (Ivens, 1978; Zabkiewicz and Gaskin, 1978), the soil can be reduced to a volume from which hand-sorting, directly or after airflow separation, can readily be achieved. Fay and Olson (1978) described a technique for seeds of *A. fatua* in which the soil is placed in nylon net bags which

TABLE I. Some procedures for separating seeds from soil

Authors	Steps in the procedure				
Hyde and Suckling (1953)	Sieving (wet)	→ Flotation (organic)	→ Airflow separation	→ Hand-sorting (dry)	→ Viability determination (germination)
Malone (1967)	Dispersion/ flotation (solution)	→ Sieving (wet)	→ Hand-sorting (dry)	→ Viability determination (tetrazolium)	
Jones and Bunch (1977)	Sieving (wet)	→ Airflow separation	→ Flotation (organic)	→ Hand-sorting (dry)	→ Viability determination (germination)
Roberts and Ricketts (1979)	Sieving (wet)	→ Flotation (water)	→ Flotation (solution)	→ Hand-sorting (wet)	→ Apparent viability determination (pressure)
Standifer (1980)	Soaking	→ Sieving (wet then dry)	→ Airflow separation (3-stage)	→ Hand-sorting (dry)	→ Viability determination (germination)

are mechanically agitated in water and the seeds then removed by hand. They quote the time required for the whole procedure as 5–26 minutes for a 3–5 kg soil sample and note that it would be applicable to other large seeds. If the seeds are very small, like those of *Orobanche* spp., sieving can remove most of the soil components (Krishna Murty and Chandwani, 1974). Ashworth (1976) described a technique for the quantitative detection of *Orobanche ramosa* in which the particle size range was first reduced to 125–495 μm by sieving, this fraction was centrifuged in calcium chloride solution (specific gravity 1.396), and the seeds were then counted directly on a filter. As few as five seeds per 500 g of soil could be reliably detected, and field infestations defined accurately.

The problem of isolating seeds is much more difficult when, as is usual, a range of species is present which differ in seed size. Sieving can then only concentrate the seeds in a fraction with a fairly large range of particle size, and although in a few soils this may permit hand-sorting (Hayashi and Numata, 1971) another step is usually needed before it becomes feasible.

2. *Flotation*

Viable seeds usually sink in water, although separation from mineral matter and some of the organic soil components can be achieved in a rotary tumbler with controlled water flow (Thorsen and Crabtree, 1977). More commonly, the soil containing the seeds is added to a liquid with a density greater than that of the seeds so that they can be skimmed off; devices which facilitate this have been described (Hayashi, 1975; Sinyukov, 1975).

Many different liquids have been used as flotation media. Solutions of mineral salts are often favoured, since they are cheap and present little health hazard. Among those used in recent studies are potassium carbonate (Hayashi and Numata, 1971), sodium carbonate (Hayashi, 1975; Rodríguez Bozán and Alvarez Rey, 1977), zinc chloride (Fekete, 1975; Hunyadi and Pathy, 1976) and calcium chloride (Barbour and Lange, 1967; Roberts and Ricketts, 1979). Soils with a high clay content may need treatment with a dispersant; sodium hexametaphosphate + sodium bicarbonate has been used, either with magnesium sulphate as the flotation medium (Malone, 1967) or prior to sieving (Carretero, 1977).

Other workers have preferred organic liquids of appropriate density, such as tetrachloromethane (Hyde and Suckling, 1953; Dechkov, 1975) or perchloroethylene (Jones and Evans, 1977). In Australia solvents such as perchloroethylene (S.G. 1.62), trichloroethylene (S.G. 1.46)

and trichloroethane (S.G. 1·31) are used to separate soil from legume seeds recovered from the soil surface, the choice depending on the species (Loch and Butler, 1977). Flammability, toxicity and the need for a reasonably high boiling point to reduce losses must be taken into account, and adequate ventilation is needed during use (Jones and Bunch, 1977; Loch and Butler, 1977).

3. Further separation

Airflow separation has been used either as a complement to flotation on liquids (Hyde and Suckling, 1953; Jones and Bunch, 1977) or as a replacement for it. Tulikov (1976) described a method in which each of a series of size fractions obtained by sieving the soil sample is placed in a seed cleaner with vertical airflow, and claimed the technique to be reliable and twice as rapid as liquid flotation. Standifer (1980) also used a vertical airflow, first removing the light seed coats and bulky debris and then increasing the velocity of flow to separate the seeds from the heavier mineral particles.

With all techniques of physical separation the final step is normally hand-sorting in which the seeds are picked out individually from the residual organic matter, either directly or after drying, under a magnifier or binocular microscope. Because seed coats are often resistant to decay they may persist for long after the seeds have died, either as fragments or as entire structures. *Stellaria media*, *Chenopodium album* and *Portulaca oleracea* are species of which large numbers of empty seed coats are commonly found (Jensen, 1969; Carretero, 1977). Their presence greatly hinders the process of hand-sorting and imposes the need for a standard of acceptable seed damage. Roberts and Ricketts (1979) included flotation in water as one step of their procedure in order to reduce the numbers of empty seed coats.

4. Determination of viability

The numbers of dead seeds present may be significant in studies of their fate or of vegetation history, but usually concern is with the viable seeds and a method of determining viability is needed. The obvious method is to place the seeds, or a random sample of them, under conditions favourable for germination. This is most likely to be effective when a single species is involved, because optimum conditions can then be given. Pre-treatments can also be applied, such as pricking for *Avena fatua* (Wilson, 1972) or scarification for seeds of legumes; comparisons of germination with and without scarification provide useful information on the proportion of "hard" seeds (Jones and Evans, 1977).

Germination tests to assess viability are less satisfactory when a range

of species is present since no single set of conditions will give a valid estimate for all of them. Other methods which have been used include direct examination of the embryo and testing with tetrazolium salts (Malone, 1967; Hayashi and Numata, 1971), but these are tedious and time-consuming when the seeds are small. One alternative is to record those seeds which appear to be intact and which resist gentle pressure, and to regard them as "apparently viable" (Zelenchuk, 1961; Hayashi *et al.*, 1978; Roberts and Ricketts, 1979). Carretero (1977) found that of the intact, apparently viable seeds of four species, 71–88% germinated when tested. For many purposes, assessment of the apparently viable seeds may be adequate.

D. COMPARISON OF TECHNIQUES

Most workers have employed the sieving/flotation technique or the seedling emergence technique, but not both. Separation by physical means would be expected to reveal many more seeds than seedling emergence because many will be non-viable, and comparisons have shown this to be so (Ramírez and Riveros, 1975; Williams and Egley, 1977). Although the percentage viability of legume seeds separated from the soil may be high (Charlton, 1977), for most species it is usually low. The value obtained depends on the criteria used in determining what to record as seeds and also on the nature of the test used to determine the viability. Mean values for viability which have been recorded include 15% (Wehsarg, 1912), 13·5% (Platon, 1955), 6–22% (Želev, 1965) and 12–36% (Carretero, 1977), while Kropáč (1966) considered that a figure of 20% could reasonably be assumed. Mean values can be misleading, however, since there is likely to be considerable variation from species to species.

In a detailed comparison with samples from 57 fields, Jensen (1969) found that separation gave an average of 135 000 seeds m^{-2} of which 27% germinated when tested after chilling and a further 11% were judged to be viable at the end of the tests. Seedling emergence gave an average estimate of 19 000 m^{-2} , only 38% of the viable seeds recovered by the separation technique. However, this difference was largely accounted for by the species with the highest seed numbers, *Juncus bufonius*, of which only 10% of the viable seeds emerged as seedlings in the glasshouse. Excluding this species, seedling emergence gave an estimate equivalent to 75% of the viable seeds recovered by separation.

The main advantages of the seedling emergence technique are that the effort required is spread over a period, each seedling represents

a viable seed, and seedlings are usually easier to identify than seeds. The main disadvantages are the delay between sampling and obtaining the results and the fact that seed banks of some species may be underestimated. The shorter the period for which the samples are kept, the greater the risk of underestimation. Nevertheless, this method has been preferred for monitoring long-term experiments (Brenchley and Warington, 1930; Roberts, 1962; Barralis, 1972) and for studying seasonal changes in the seed bank (Guevara and Gómez-Pompa, 1972; Young and Evans, 1975). For some purposes it may not be necessary to attempt complete enumeration of the seeds present. If the aim is simply to determine whether species form seed banks which persist from year to year, or to detect gross changes in seed numbers within the year, a short germination period under standard conditions may prove adequate (Grime, 1979; Thompson and Grime, 1979).

The main virtue of techniques involving physical separation of seeds from the soil is that the results are available as soon as processing is complete; this is particularly desirable if the information is to be used predictively (Carretero, 1977). Unless viability is determined, however, these methods greatly overestimate the potential flora. Which technique is employed depends largely on the nature and purpose of the investigation; some workers have used a sequence involving seedling emergence followed by sieving and the tetrazolium test (Johnson, 1975; Moore and Wein, 1977). Results obtained by separation techniques are often quoted in terms of total seeds, but are sometimes adjusted for viability. Because of the differences in the methods used care is needed in making quantitative comparisons of results obtained by different investigators.

III. SEED BANKS OF ARABLE SOILS

Because of the obvious economic importance of arable weeds and the fact that many of them reproduce only by seeds, considerable attention has been paid to the seed banks of cultivated soils. Published investigations can be considered under three headings. Firstly, there are those of a "survey" nature in which determinations have been made of the seeds present in the soil of fields in a particular locality or over a wider area. Secondly, there are those in which the seed bank has been used as an index to monitor improvements in agrotechnical measures or to compare the effects of different crop rotations, cultural techniques or weed control practices. Finally, there have been limited investigations of the quantitative relationships between the seed bank and the weed vegetation developing after cultivation.

A. SURVEYS

The main conclusion from the early work reviewed by Kropáč (1966) was that the numbers of seeds present in arable soils are usually very high. Data from various sources which were tabulated by Jensen (1969) show that the average number of viable seeds in the plough depth (0–15 or 0–25 cm) is usually greater than 4000 m^{-2} and in very weedy fields may be as high as 70000 – 80000 m^{-2} .

Recent studies confirm the generally high level of infestation by weed seeds. One of the most extensive series of investigations is that of Dechkov (1974, 1975, 1976, 1978), covering more than 800 fields in various regions of Bulgaria. Although the species composition of the seed bank varied according to soil type and district, certain species were particularly well represented. These included *Amaranthus* spp., which accounted for more than 50% of all seeds found in the western Danube Plain, and *Echinochloa crus-galli*. Others which occurred widely in appreciable numbers were *Digitaria sanguinalis*, *Setaria* spp. and *Sinapis arvensis*. Another extensive survey covering some 800 spring cereal fields was made in Finland (Paatela and Erviö, 1971) and showed a high general level of infestation. Although there were differences between districts and between soil types the ten most abundant species, which included *Chenopodium album*, *Spergula arvensis*, *Ranunculus* sp., *Galeopsis* sp., *Viola arvensis* and *Stellaria media*, accounted for 90% of all seeds found. Seed numbers, especially of *Chenopodium album* and *Stellaria media*, were highest following potato and root crops and least after leys. Raatikainen and Raatikainen (1972) discussed the same data from the point of view of the length of time for which the fields had been under arable cultivation. They concluded that seed numbers in general increased with the period of cultivation, while those of *Carex* spp., present before clearance, decreased with time.

A survey of 57 fields in Denmark by Jensen (1969) gave an average value of 50250 viable seeds m^{-2} in 0–20 cm, with a range from 600 to 496000 m^{-2} . The seven most common species, *Chenopodium album*, *Gnaphalium uliginosum*, *Juncus bufonius*, *Plantago major*, *Poa annua*, *Spergula arvensis* and *Stellaria media* accounted for 78% of all the seeds recorded. In Great Britain a survey of 58 vegetable fields gave a range of 1600– 86000 viable seeds m^{-2} in 0–15 cm, with a median value of 10000 m^{-2} (Roberts and Stokes, 1966). The seven most common species, *Poa annua*, *Stellaria media*, *Urtica urens*, *Senecio vulgaris*, *Capsella bursa-pastoris*, *Chenopodium album* and *Veronica persica*, accounted for 80% of the seeds found. Samples from 32 cereal fields in the English Midlands gave a range of 1800– 67000 viable seeds m^{-2} in 0–15 cm with a median of 5500 m^{-2} ,

and *Poa annua*, *Polygonum aviculare*, *Stellaria media*, *Chenopodium album* and *Aethusa cynapium* were the species most frequently represented (Lockett and Roberts, 1976).

Dvořák and Krejčíř (1974) examined fields of wheat, maize, sugar beet and lucerne in Czechoslovakia and showed that of the seeds found *Chenopodium album* accounted for 50%, *Stellaria media* for 14% and *Sinapis arvensis* for 10%. Other recent studies include those by Fekete (1975) and Sárkány (1975) of maize fields in Hungary, where *Echinochloa crus-galli* was the main species, and by Kazantseva and Tuganaev (1972) in the Tatar ASSR who recorded *Chenopodium album*, *Polygonum aviculare*, *P. convolvulus*, *Stachys annua* and *Amaranthus retroflexus* as major contributors to the seed bank. *A. retroflexus*, *Echinochloa crus-galli* and *Sinapis arvensis* were three of the main species represented in seed banks of cereal fields in Romania (Pocinoc, 1969) and in Spain the viable seeds in five fields ranged from 1000–21000 m⁻² with *Portulaca oleracea* the most abundant species (Carretero, 1977). A maize field in Argentina had 90600 viable seeds m⁻² in 0–20 cm, with *Portulaca oleracea* and *Chenopodium album* the main species (Leguizamón and Cruz, 1980) while two other arable fields had approximately 4000 m⁻², mainly *Amaranthus quitensis*, *Chenopodium album*, *Digitaria sanguinalis* and *Echinochloa* spp. (Leguizamón *et al.*, 1979).

These results are in accord with earlier investigations, summarized by Kropáč (1966), in showing that the main contributors to seed banks of arable soils are annual weeds. These often account for 95% or more of all seeds, and those of perennial weeds and crop species are usually only poorly represented. Moreover, there are often one or two species which have seed numbers much greater than the rest and a fairly small number of species normally accounts for about 80% of all seeds found, even when the fields sampled are distributed over a region. In cool temperate areas such as northern Europe, *Chenopodium album* and *Stellaria media* are among the species consistently found to be major contributors to arable seed banks. In areas with higher summer temperatures, *Amaranthus* spp. and *Echinochloa crus-galli* are among those of which high numbers of seeds are generally found.

Many of the studies of arable fields have included determinations of the numbers of seeds present at different depths in the soil (e.g. Kropáč, 1966; Dvořák and Krejčíř, 1974; Fekete, 1975). Where the soil is regularly worked to the same depth, the distribution of seeds tends to be fairly uniform throughout that depth with only a few seeds below it. However, much depends on the time of cultivation in relation to major recent seed inputs, on the depth of cultivation, and on whether or not the soil is wholly or partially inverted. If weeds have seeded

and the land is then ploughed, the seeds may be concentrated in a zone at depth; Kazantseva and Tuganaev (1972) found a direct correlation between the vertical distribution of seeds and the depth of ploughing. A detailed study of the distribution of seeds of *Tribulus terrestris* showed that the numbers varied inversely and linearly with depth, but that soil type, texture and method of cultivation affected the gradient of distribution (Goeden and Ricker, 1973). The very small seeds of *Striga asiatica* were concentrated in the upper 30 cm of a sandy soil, but some were found even at a depth of 1.5 m and the percentage viability was higher in seeds which were deeply buried (Robinson and Kust, 1962).

The very limited data for tropical arable soils indicate that these too contain large numbers of viable weed seeds. Vega and Sierra (1970) sampled a lowland rice field in the Philippines and found 80000 m^{-2} in 0–15 cm; the highest numbers were those of *Fimbristylis miliacea* and other Cyperaceae, which accounted for 94% of all the seeds found. A rice field in Java sampled in the dry season had more than 20000 viable seeds m^{-2} in 0–10 cm, almost all Cyperaceae (Hayashi *et al.*, 1978). Kellman (1974b) recorded an average of 7600 viable seeds m^{-2} in 0–4.2 cm of arable fields in Belize, with *Amaranthus spinosus* a notable contributor. In further samples from 0–10 cm in a maize field there were 9800 m^{-2} , mainly concentrated near the surface (Kellman, 1978). A study of peat soil in Malaysia which had been cropped with pine-apples for periods of 6 months to 10 years revealed only small numbers of viable seeds ranging from $70\text{--}630\text{ m}^{-2}$, but the numbers of fern spores present were almost ten times greater than this (Wee, 1974).

B. EFFECTS OF CULTURAL PRACTICES

The seed bank reflects the history of the land in terms of cropping and the extent to which the cultural practices associated with the crops have been successful in controlling weeds and limiting their seed production. The weed vegetation present at any one time is only a partial representation of the potential weed flora (Rola, 1962), but assessment of the seed bank provides a means of determining long-term changes in the overall level of weed infestation and in the relative abundance of the different seed-producing species. Some examples of the reductions in numbers of seeds achieved in particular circumstances are shown in Table II.

Roberts (1962) showed that in the absence of significant production of fresh seeds, the numbers of viable seeds of arable weeds in a soil subject to frequent cultivation decreased exponentially. The rate of

TABLE II. Some reductions in size of seed banks of arable soils brought about by cultural treatments

Location	Cultural treatment	Period (years)	Reduction (%)	Authors
Bulgaria	Crop rotations; herbicides	6	65	Dechkov and Atanassov (1976)
Hungary	Maize; improved techniques; herbicides	10	75	Fekete (1975)
France	Sunflower, wheat, barley; herbicides	5	33	Barralis <i>et al.</i> (1978)
	Sugar beet, wheat, barley; herbicides	4	63	
England	Fallow; four cultivations per year	5	87	Roberts and Dawkins (1967)
	Fallow; two cultivations per year	5	83	
	Chemical fallow	5	71	
England	Fallow; seven cultivations per year	4	97	Roberts and Feast (1973b)
	Fallow; two cultivations per year	4	89	
	Chemical fallow	4	81	
USA	<i>Abutilon theophrasti</i> ; lucerne	5	61	Lueschen and Andersen (1978)
	<i>Abutilon theophrasti</i> ; fallow; two ploughings per year	5	93	
	<i>Abutilon theophrasti</i> ; chemical fallow	5	73	
USA	<i>Brassica kaber</i> ; bromegrass	4	40	Warnes and Andersen (1978)
	<i>Brassica kaber</i> ; fallow; three ploughings per year	4	93	
	<i>Brassica kaber</i> ; chemical fallow	4	45	
USA	Maize; herbicides	3	67	Schweizer and Zimdahl (1979)
	Maize, sugar beet, barley; herbicides	3	49	
USSR	Vegetable crops; herbicides, ploughing	3	52	Kolesnikov and Sidorov (1974)
USSR	Cotton; herbicides	4	83	Lozovatskaya (1968)

decline varied with the species and also with frequency of cultivation. When soil was cultivated monthly during the growing season the annual loss was almost 60% (Roberts and Feast, 1973b). In another experiment the seed bank in 0–23 cm declined at a rate of 36% per year with four cultivations annually and 22% per year with none at all (Roberts and Dawkins, 1967). The results for *Abutilon theophrasti* and *Brassica kaber* (Table II) suggest comparable loss rates. The seed population in a very shallow layer of cultivated soil would be expected to decline

more rapidly (Roberts and Feast, 1972). In an experiment in Louisiana, continuous cropping for two years without ploughing eliminated viable seeds of *Eleusine indica* from 0–5 cm and reduced those of *Cyperus iria* by 76%, although there was much less effect on those at 15–20 cm (Standifer, 1980). Jan and Faivre-Dupaigne (1977) found that where effective weed control was achieved on direct-drilled plots, the numbers of viable seeds in 0–5 cm were reduced by 39% and 68% in two three-year experiments.

In practice, it is difficult to ensure that all seeding by weeds is prevented, and the addition of fresh seeds can easily counterbalance the natural losses from the seed bank (Roberts, 1962). Data quoted by Kropáč (1966) and Roberts (1970) show that fallowing, when properly carried out, can bring about appreciable reductions in the seed bank. With traditional methods of cropping, however, the evidence shows that only moderate reductions could be achieved over relatively long periods. Modern selective herbicides allow more complete weed control, so that the natural losses are cumulative and the seed bank can be substantially reduced within a few years (Table II).

Individual herbicides rarely kill all the weed species that may be present when applied at rates which are selective in a crop. If the same crop/herbicide combination is repeated, seed inputs from those species which survive may soon drastically alter the composition of the seed bank. Fekete (1975) recorded an increase in seeds of *Echinochloa crus-galli* where atrazine was used in maize, while Zuza (1973) showed that the use of triazine herbicides and 2,4-D in proso millet reduced seed numbers of dicotyledons but that 2,4-D in particular increased those of grasses. Results from an experiment in Germany in which various weed control measures had been applied to the same cereal plots for 12 years were reported by Hurle (1974). With no control at all, there were 43800 viable seeds m^{-2} in 0–25 cm. The best treatment, DNOC, gave a value only 40% of this while those for MCPA, 2,4-D, calcium cyanamide and harrowing were 64, 56, 61 and 68% respectively. The effect of rotating these treatments was less than expected; the weak link, harrowing, allowed the greatest seed set and this reduced the benefits from previous treatments. Other investigations in which seed bank determinations have been used to assess the effects of herbicide treatments include those of Everest and Davis (1974), Dale and Chandler (1976, 1977) and Burnside (1978).

Estimates of seed numbers have also been made in experiments involving crop rotations and fertilizers (Watanabe and Ozaki, 1964; Dotzenko *et al.*, 1969; Dechkov and Atanassov, 1976). These show, as might be expected, that changes in the numbers of seeds of the

different weed species reflect opportunities for seed production under the various regimes. In an experiment in Oklahoma in which different fertilizers had been applied to winter wheat for 47 years, the lowest numbers of seeds were found on the unfertilized plots, and they increased as the fertilizer treatments became more complete (Banks *et al.*, 1976). As in earlier work in Britain (Brenchley and Warington, 1930), some species were favoured by particular fertilizer treatments.

Two experiments with raspberries also illustrate the way in which seeds can accumulate under particular regimes. Allott (1970) found that after eight years there were 1780 viable seeds m^{-2} in 0–10 cm where plots had been cultivated, but only 240 m^{-2} where a herbicide programme had been used. Clay and Davison (1976) established an experiment on land which had previously been under grass with 1300 viable seeds m^{-2} in 0–15 cm. On cultivated plots, annuals such as *Capsella bursa-pastoris*, *Stellaria media* and *Poa annua* were able to set seed between cultivations and after 8 years there were 14 700 seeds m^{-2} . In contrast, there was little change during this time in the numbers of seeds on bare plots which received herbicides.

C. RELATIONSHIPS WITH THE FLORA AFTER CULTIVATION

Relatively little attention has been devoted to the quantitative relationships between seed banks in arable soils and the populations of weed seedlings that appear after the ground has been disturbed. Von Hofsten (1947) recorded good correlation between the numbers of plants of *Sinapis arvensis* and the numbers of seeds in the soil at points on a grid over a single field. Chancellor (1965) noted that one very dense stand of *Matricaria matricarioides* accounted for only about 4% of the seeds in the soil, while Barralis (1965) found that in a crop of winter wheat the weeds that appeared represented 2·5% of the viable seeds present in 0–10 cm. Assessments made more recently (Table III) confirm that the seedlings account for only low percentages of the viable seeds present.

Variation in the percentage of viable seeds giving rise to seedlings can arise from several sources. The general suitability of the conditions for germination is obviously important; if it is very dry, for example, few, if any, seedlings may establish. The physical condition of the surface soil can also affect the numbers of seedlings, and twice as many may appear on a fine, firm seedbed as on a rough one (Roberts and Hewson, 1971). Soil disturbance acts selectively on the seed bank, since the prevailing conditions are likely to meet the germination requirements of some species but not others. Many species show distinct

TABLE III. Numbers of seedlings of weed species emerging in crops in relation to the numbers of viable seeds of those species present in the soil

Location	Crop	Depth (cm)	Seedlings as % of viable seeds	Authors
Spain	Winter crops	10	3.4	Carretero (1977)
	Summer crops	10	1.7–10.4	
France	Winter wheat	10	1.9–13.3	Barralis (1972)
France	Winter and spring cereals; mean	10	5.3	Barralis and Salin (1973)
	Winter wheat	10	0.6–8.9	
France	Spring barley	10	3.7–8.6	Chadoeuf (1976)
	Winter wheat	10	3.0–10.8	
France	Spring barley	10	5.8–15.3	Barralis <i>et al.</i> (1978)
	Seedbeds throughout the year; median	10	2.0	
England	Cereals	25	1	Hurle (1974)
USA		20	2.4	Williams and Egley (1977)

patterns in the seasonal distribution of seedling emergence and the species composition of the plant population is likely to be influenced by the time of year at which the soil is disturbed. This is shown strikingly by the data of Carretero (1977). Comparisons of seed banks and resulting weed floras showed that the species could be divided into two groups, one of which produced no seedlings in summer crops, the other none in winter crops. The overall ratio between the numbers of viable seeds and the numbers of seedlings that appeared thus depended both on the time of cultivation and on the proportions of seeds of the two groups present in the soil.

Variation will also arise if species differ appreciably in the percentages of seeds which give rise to seedlings under optimum conditions, and there is evidence that this is so. Carretero (1977) showed that whereas the percentages were always low for *Chenopodium album* and several other species, they tended to be much higher for *Setaria adhaerens*. In one summer crop, about 22% of the viable seeds of this species in 0–10 cm produced seedlings. Roberts and Ricketts (1979) also recorded low percentages for *Chenopodium album*; usually less than 4% of the viable seeds in 0–10 cm produced seedlings even at the season of peak emergence. For *Papaver rhoeas* and *P. dubium* the percentages were even less, no more than 1% at the times of year most favourable for emergence. In contrast, the seedlings of *Polygonum aviculare* emerging

after spring cultivation accounted for up to 15% of the viable seeds. Seed size evidently plays some part in these differences between species (Carretero, 1977). Although cultivation may bring about germination of a proportion of the seeds throughout the disturbed layer (Kropáč, 1966), only those within a certain distance of the surface will have sufficient reserves to enable them to reach it. For the large-seeded *Avena fatua*, percentages higher than any mentioned above have been recorded (Wilson and Cussans, 1975).

The age of the seeds may be an additional source of variation. Many species of arable weeds, such as *Senecio vulgaris*, *Stellaria media* and *Urtica urens*, produce seeds of which a variable but often appreciable proportion is capable of immediate germination under suitable conditions. If seeds of very recent origin form a significant part of the total bank, the percentages giving rise to seedlings might thus be relatively high. Using a "mark-and-recapture" technique Naylor (1972) found that about 60% of the seedlings in populations of *Alopecurus myosuroides* were derived from seeds less than one year old. The converse may be true if seeds have a high level of initial dormancy. In a detailed study of *Avena fatua* Wilson and Cussans (1975) showed that when the seeds were mainly those shed in the previous crop, 17–24% of those present in 0–20 cm in February produced seedlings in the spring barley crop. Where no fresh seeding had taken place, 38% of the seeds present gave rise to seedlings.

TABLE IV. Numbers of seedlings emerged per year in relation to the numbers of viable seeds in 0–23 cm at the start of the year (from Roberts and Dawkins, 1967)

Cultivations per year	Seedlings as % of viable seeds					
	Year 1	Year 2	Year 3	Year 4	Year 5	Year 6
4	10.7	6.1	9.4	8.3	8.7	9.6
2	7.8	4.7	6.7	6.1	9.0	7.2

Roberts and Dawkins (1967) made successive annual determinations of the naturally-occurring viable seeds in field plots and assessed the total numbers of seedlings appearing in each year, allowing no fresh seeding to take place. Under consistent regimes of soil disturbance there were no systematic trends in the percentages of seeds giving rise to seedlings (Table IV), and the chances of a seed producing a seedling remained the same over the six-year period. Seely (1976), however, has suggested that sometimes estimates of seeds in the soil may give an erroneous impression of the potential contribution to the flora. He

cites an example in which a reduction in seed numbers of *Spergula arvensis* by 97% took place over 12 years, whereas 97% reduction in seedlings occurred after 6–7 years and after 12 years the seedling population was less than 0·5% of that originally present. Data from experiments in which seeds of annual weeds were mixed with soil which was then regularly disturbed also showed that the decline in seedling numbers from year to year was somewhat more rapid than that of viable seeds (Roberts and Feast, 1973a). Estimates of the chances of a seed producing a seedling in a variety of situations have been compiled and discussed by Sagar and Mortimer (1976), and related aspects considered by Roberts (1972).

A question which has aroused some interest in recent years is whether data on seed banks can be used predictively to forecast weed problems and help in specifying control measures. The knowledge that a particular species is present as a major component of the seed bank can itself be useful. In Bulgaria, Dechkov (1974, 1975, 1976, 1978) mapped the main species present in his surveys and was able to indicate the areas in which particular herbicides would be needed to give effective weed control in the maize crop. Seed bank data obtained from year to year can also be valuable in monitoring the overall success of weed control programmes and in suggesting improvements.

Several attempts have been made to determine whether the weed flora in crops to be sown at different times of year can be predicted from the presence of seeds in the soil. Lhoste *et al.* (1969) set out paired 1 m² plots, recovered the top 5 cm of soil from one of each pair, recorded the seedlings that emerged in the glasshouse, and then compared the result with field emergence in June and November on the remaining plots. Although there was good correspondence for some species, there were others which emerged in the field but not in the glasshouse and vice versa. They concluded that the technique was promising, and might be improved by reproducing the appropriate climate in the glasshouse. Naylor (1970) related seedling emergence from soil samples in the glasshouse to subsequent field emergence in a study of *Alopecurus myosuroides* and obtained reasonable correlation.

The possibility of using determinations of seeds in soil samples as an advisory tool has been examined in Texas by Palmer *et al.* (1970). They listed a number of advantages that the information could confer, but conceded the need for better sampling methods, a better way of determining viability, and for an assessment of the economics of the technique as a self-sustaining service. Determinations of the seed content of *Amaranthus* spp. have since been used as a basis for suggesting weed control methods in future cropping plans (R. D. Palmer, pers. comm.).

Prediction of weed infestations has also been examined in the USSR (Artyushin and Libershtein, 1976).

If the relative numbers of seeds of different species are determined, some estimate of the composition of the weed flora after cultivation at different times of year could be made from the known seedling emergence patterns in the region concerned. However, this would not allow for the inherent differences between species in the percentage of seeds likely to produce seedlings which have already been mentioned. In an attempt to include this factor, Roberts and Ricketts (1979) derived empirical curves by plotting the percentages of seeds in 0–10 cm producing seedlings against the date of cultivation. If sufficient data were available, it would be possible to predict seedling numbers at any time of year from the numbers of seeds and the expected percentage emergence obtained from the curves. As previously mentioned, lack of soil moisture limits germination on some occasions and not on others, so that the estimates of seedling numbers would be subject to considerable error. Provided that this factor does not operate selectively to a major extent, however, it might at least be possible to forecast the relative contributions of different species to the seedling flora, and this could be of practical value.

IV. SEED BANKS OF GRASSLANDS

The reserves of seeds in soils beneath different meadow and pasture types have been the subject of investigations in Europe and North America (e.g. Chippindale and Milton, 1934; Dore and Raymond, 1942; Prince and Hodgdon, 1946; Champness and Morris, 1948; Milton, 1948; Foerster, 1956; Zelenchuk, 1961; Golubeva, 1962). Much of this work has been reviewed elsewhere (Major and Pyott, 1966; Rabotnov, 1969) and will not be considered in detail here. As might be expected, the data show wide variation in the numbers of viable seeds found. Examples from published accounts of work in Great Britain listed by Thompson (1978) range from approximately 400 m^{-2} in a permanent pasture to 70000 m^{-2} in a pasture which was formerly arable, and results from the USSR also show a wide range (Rabotnov, 1978).

As already emphasized, because of differences in the depth of sampling and technique of estimation, comparisons between the results of different workers must be made with care. The time of sampling in relation to seed production is particularly important, and the annual grassland in California studied by Bartolome (1979) provides a striking illustration of this (Fig. 1). At the start of the growing season there were more than $60000 \text{ seeds m}^{-2}$ but the numbers declined rapidly

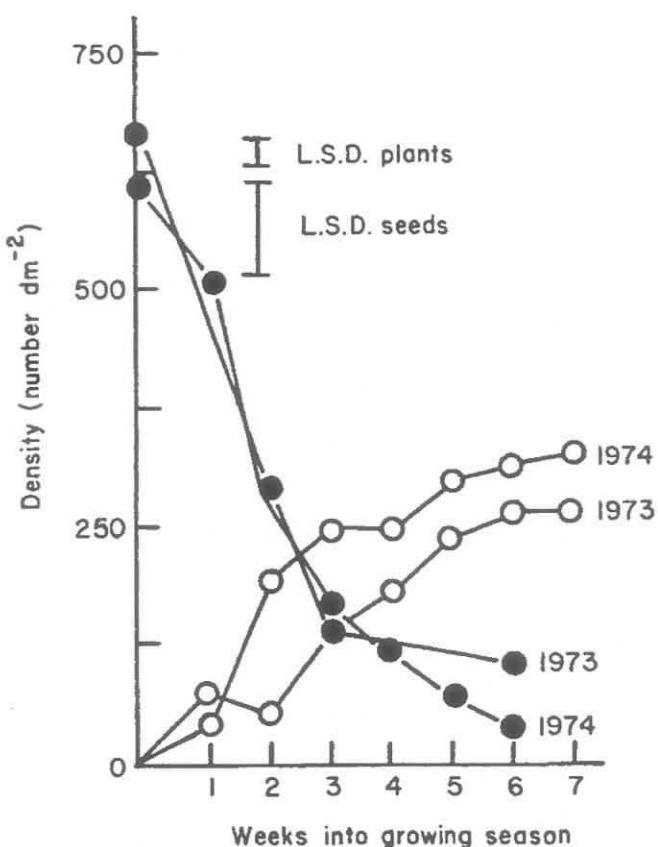


FIG. 1. Changes in total plant density (\circ) and numbers of germinable seeds in the soil (\bullet) of a California annual grassland. The first soil sample was collected in late summer before the autumn rains (from Bartolome, 1979).

as germination took place after the autumn rains. Nevertheless, it appeared that many of the species carried over some viable seeds from year to year and these would be important for survival if drought were to occur during the growing season.

A. GRASSES

The species composition of grassland seed banks is of greater significance than the total number of seeds present, and some examples of the relative contributions made by four groups of species to the seed reserves of a range of grassland types are listed in Table V. Although seeds of grasses often form an appreciable percentage of the total, most workers have commented on the lack of quantitative correspondence between the representation of the different species in the sward and that in the seed bank. This reflects differences among species not only in seed production, but also in seed dormancy and survival. As Grime (1979) has pointed out, in habitats subject to summer drought viable

TABLE V. Contributions of different groups of species to the viable seed banks of some grassland soils

Location	Grassland type	% of total viable seeds				Authors
		Grasses	Legumes	Rushes	Others + sedges	
Wales	Lowland grazed, reseeded <i>Lolium perenne</i>	42	3	34	21	Jalloq (1975)
	Upland grazed, reseeded <i>Lolium perenne</i>	34	7	4	55	
Wales	Acidic pasture	62	0	1	37	King (1976)
Netherlands	Pastures; mean for 73 sites	62	0.5	11	26	van Altena and Minderhoud (1972)
Germany	Permanent grass; mean for 12 sites	46	3	7	44	Foerster (1956)
S. Bohemia	Meadows, peat soils; mean % for 8 sites	27	5	13	55	Mika (1978)
USSR	Meadow-steppe; mean of mown and unmown	2	7	1	90	Golubeva (1962)
USSR	Meadows and woodland pastures; mean % for 10 sites	23	2	25	50	Pyatin (1970)
Quebec	Permanent pasture; mean % for 4 sites	22	0.6	40	37	Dore and Raymond (1942)
California	<i>Stipa pulchra</i> ; mean of grazed and ungrazed	36	2	0	62	Major and Pyott (1966)
Argentina	Old pasture	8	8	25	59	Leguizamón and Cruz (1980)
Tasmania	<i>Poa gunnii</i> grassland	16	0	35	49	Howard (1974)
Surinam	<i>Axonopus compressus</i> ; grazed, mean for 2 sites	3	0.1	41	56	Dirven (1966)

seeds of many grasses are present only during the dry season; they are capable of germination under a wide range of conditions and moisture supply is the main factor determining the time of germination. Except during the summer period, therefore, seeds of these species make little or no contribution to the seed bank. Practically all the seeds germinate in autumn and large numbers of seedlings appear on bare ground which has developed in the dry season. Not only is this true for annual grassland (Fig. 1), but some of the commonest grasses of

meadows and pastures in Europe show this pattern (Grime, 1979; Thompson and Grime, 1979). They include not only annuals such as *Hordeum murinum*, *Bromus sterilis*, *B. mollis* and *Lolium multiflorum*, but also perennials. Among them are desirable species which are frequently sown, such as *Dactylis glomerata*, *Festuca ovina*, *F. pratensis* and *Lolium perenne*. Surveys consistently demonstrate the absence of appreciable numbers of viable seeds of these species from the buried seed population (Chippindale and Milton, 1934; Champness and Morris, 1948; Foerster, 1956; Thompson and Grime, 1979). Van Altena and Minderhoud (1972) found that although *Lolium perenne* was a major component of pastures in the Netherlands, in terms of viable seeds present it ranked only seventh among the grasses and the numbers were low. Only very few seeds or none at all were recorded for other common sward components such as *Dactylis glomerata*, *Hordeum secalinum*, *Festuca pratensis* and *F. rubra*. The fact that these species do not accumulate reserves of buried seeds is of great importance for pasture management since it means that sown species, and *Lolium perenne* in particular, tend to be replaced by indigenous grasses (Chancellor, 1978; Grime, 1979; Thompson and Grime, 1979).

Many of these indigenous grasses, in marked contrast to the species cited above, produce seeds which do not germinate synchronously and of which a proportion can survive for at least a year when buried. Investigations of pastures and meadows in northern Europe consistently show that *Agrostis stolonifera*, *A. tenuis*, *Poa annua* and *P. trivialis* tend to be major contributors to the seed bank even though they may be present to only a limited extent in the vegetation (Chippindale and Milton, 1934; Champness and Morris, 1948; Foerster, 1956; Delpech, 1969; Rabotnov, 1969; van Altena and Minderhoud, 1972; Sparke, 1979). These species are thus well-placed to exploit gaps arising in the sward through death of the sown species, trampling and poaching by livestock or other disturbances. McRill (1974) showed that *Agrostis* spp., *Poa* spp. and *Holcus lanatus* were major components of the seed flora of earthworm casts from grasslands in North Wales, and argued that by providing a break in a closed community the casts could act as foci for invasion. Jallop (1975) examined the possible role of molehills in this connection and recorded a high percentage of grass seeds in molehill soils from reseeded *Lolium perenne* pastures (Table V). Seeds of *Agrostis* spp. were prevalent in soil from upland sites, and those of *Poa annua* in lowland soils; the sown species accounted for less than 3% of the seeds found. Douglas (1965) considered the seed bank in relation to sward renewal and concluded that because of the absence of viable seeds, desirable grasses already present would not contribute

to the new sward. Where *Poa* spp., *Agrostis* spp. and *Holcus lanatus* occurred in the vegetation, however, the presence of viable seeds in the surface layer of soil would be expected.

The lack of correspondence in representation of grass species in the vegetation and in the seed bank was very evident in the California grassland studied by Major and Pyott (1966), where no seeds of the dominant species, the perennial *Stipa pulchra*, were found in the soil. Dirven (1966), however, found that in two heavily grazed *Axonopus compressus* pastures in Surinam almost all the grass seeds recorded were of this species, although they accounted for only 3% of the total seed bank. Grasslands in Japan studied by Hayashi and Numata (1971, 1975) illustrate the differing relationships between the composition of the vegetation and that of the seed reserves. In pasture dominated by *Zoysia japonica* and other species regenerating both vegetatively and by seed, there were high numbers of seeds in the soil and good correlation between the floristic composition of the sward and the seed bank. The dominants of tall-grass meadows, *Miscanthus sinensis* and *Arundinella hirta*, however, regenerate mainly vegetatively and few seeds of these were recorded in the soil.

B. LEGUMES

Leguminous species are of particular interest as components of grassland seed banks because of their forage value. Krylova (1979) has summarized the published data obtained in the USSR and concluded that even in meadows of the forest zone, where the seeds are mainly in the top 5 or 10 cm of soil, the numbers are less than those of the herbs, grasses and sedges. As with other meadow species, seed numbers tend to be greater in wet soils than in dry ones and in flooded meadows there were up to 520 viable seeds m^{-2} , equivalent to 5.7% of all the viable seeds present. In pastures or grassland under seasonal grazing, the commonest leguminous species was *Trifolium repens*, with up to 1700 seeds m^{-2} . This is true elsewhere in Europe (Foerster, 1956; van Altena and Minderhoud, 1972); Champness and Morris (1948) record *T. repens* as one of the species which had a markedly greater representation in the seed bank than in the composition of the sward.

In most grassland types, the numbers of seeds of legumes tend to be low compared with those of other groups of species (Table V). Appreciable seed banks of *Ulex* spp. can occur, however, where seeding has taken place over a long period. Numbers of viable seeds at five sites in New Zealand ranged from 130 to 20500 m^{-2} , mainly in the 0–6-cm layer (Zabkiewicz and Gaskin, 1978), while Ivens (1978)

recorded 10000 m⁻² in 0–15 cm from a 20-year-old stand of *U. europaeus* in New Zealand. Viable seeds have been found up to 26 years after clearing (Moss, 1959), and in an eight-year-old *Lolium perenne* pasture in Wales seeds in *Ulex* spp. accounted for 11% of the total seed bank (Jalloq, 1975).

The occurrence of legume seeds in the soil of pastures in New Zealand has been reviewed by Suckling and Charlton (1978), who quote the ranges of seed levels for five species in areas of differing soil and climate. In lowland pastures the mean values for viable seeds of *Trifolium repens* in 0–5 cm ranged from 6·5 to 16·5 kg ha⁻¹ (915–2320 m⁻²) while those for *T. dubium* sometimes exceeded 50 kg ha⁻¹ (10000 m⁻²). There were also high numbers of seeds of this species in unploughable hill pastures, whereas those of *T. repens* were generally low and the seed levels of the other species were related to the annual rainfall. Grazing management also had an effect in determining the numbers of viable seeds in the soil.

Charlton (1977) examined the occurrence of seeds of legumes in an area of hill pasture in New Zealand and found that *Trifolium dubium* and *T. repens* were the main species, with mean values of 2540 and 290 m⁻² respectively in 0–8 cm. The viability of seeds recovered from the soil was almost 100%, although 82% of *T. dubium* and 96% of *T. repens* seeds were hard. It was concluded that buried seeds are of high value both in maintaining and increasing the legume content of hill swards. Work in Queensland has also shown that high numbers of viable legume seeds can accumulate under pasture (Jones and Jones, 1975). At the end of a four-year grazing trial comparing *Trifolium semipilosum* and *T. repens* there were 8400 and 4900 m⁻² respectively in 0–5 cm, although seedling regeneration was greater in *T. repens*.

Legume species used in subtropical pastures may also develop appreciable seed banks. Studies on 10-year-old pastures in Queensland gave an average number of 4700 m⁻² in 0–5 cm for *Lotononis bainesii*, even though this species had been only a minor component of the vegetation for some years (Jones and Evans, 1977). Most of these seeds were hard, suggesting that loss of hard-seededness is a slow process. There were also 1300–3700 viable seeds m⁻² of *Trifolium repens*, of which 70% were hard. Of the 150–500 m⁻² seeds of *Desmodium intortum* found, only 9% were hard and there were no seeds where this species had been absent for some years in the heavily grazed areas. These results show that in mixed-legume pastures large reserves of viable seeds can accumulate which are not directly related to the current vegetation.

The role of seed reserves in the maintenance of pastures in Queensland based on the tropical legume *Macroptilium atropurpureum* has been

studied in some detail. Data summarized by Tothill and Jones (1977) show that mean numbers of viable seeds of this species grown in association with different grasses ranged from 20 to 520 m⁻² in 0–5 cm. Seed numbers were lowest under heavy grazing (Jones, 1979), and it is suggested that lenient grazing in the first year is desirable in order to establish a reserve of seeds in case, from necessity, the pasture has to be overgrazed at some future time (Jones and Jones, 1978).

Although the presence of viable seeds of legumes can be beneficial for pasture maintenance, problems can arise if circumstances make it necessary to reseed with a different species or cultivar. When *Trifolium subterraneum* cv. Yarloop pastures in Australia were reseeded with other cultivars, reversion often occurred in the following year. Beale (1974) showed that seed levels of cv. Yarloop at sites sown 8–13 years previously ranged from 3 to 169 g m⁻² in 0–7.5 cm. When seeding was prevented in permanent quadrats, numbers fell by 74% in 2 years, probably largely as a result of predation. He concluded that several years with virtually no seeding would be needed to reduce the numbers to an acceptable level, although since most were near the surface ploughing down to a depth from which emergence could not occur might be feasible.

Suckling and Charlton (1978) pointed out that while seed populations of legumes can be reduced by cultivation, at least four years is required before returning to pasture. They cited an example of contamination of a seed production crop of *Trifolium repens* by *T. dubium*; after four years of arable cropping there were still 150 viable seeds m⁻² of *T. repens* and 1600 m⁻² of *T. dubium*. This species is especially serious as a contaminant of *T. repens* since the seeds are of similar size. Even more serious is the possibility of contamination of seed crops by different genotypes or cultivars of the same species, and in New Zealand areas for the production of breeders' seed are now checked for buried seeds (Suckling and Charlton, 1978).

C. OTHER SPECIES

Species of rushes (Juncaceae) and sedges (Cyperaceae) are frequently recorded as major contributors to seed banks in a range of grassland types. Rabotnov (1969) commented on the abundance of seeds of *Juncus* spp., especially *J. bufonius*, and of *Carex* spp. in meadow soils of the USSR. Seeds of *J. bufonius* were also found in most pasture soils in the Netherlands, often in high numbers (van Altena and Minderhoud, 1972). Champness and Morris (1948) recorded only low seed populations in the better types of British grasslands, but high numbers were

found where rushes and sedges occurred in the vegetation; in one upland field dominated by rushes 11000 viable seeds m^{-2} were recorded, mainly *Juncus effusus*. In a marshy area in Wales more than 50000 viable seeds m^{-2} of *Juncus* spp. were found in 0–23 cm (Anon., 1967), while 8000–9000 m^{-2} in 0–10 cm were recorded for a pasture in Romania (Simtea, 1971). Species of Cyperaceae have been reported as important contributors to seed banks in diverse temperate and tropical grasslands in Tasmania (Howard, 1974), Japan (Hayashi and Numata, 1975), Surinam (Dirven, 1966) and Belize (Kellman, 1978).

One of the most consistent features evident from the investigations of grassland seed banks is the presence of appreciable numbers of viable seeds of dicotyledonous species (Table V). Some of these are typical grassland plants; in northwestern Europe, for example, *Ranunculus repens*, *Galium saxatile* and *Cerastium holosteoides* are frequently recorded as contributors to the seed bank. In the Netherlands, *Sagina procumbens* occurred in half of the fields sampled and the average numbers were high (van Altena and Minderhoud, 1972). In moorland soils, large populations of viable seeds of *Calluna vulgaris* can accumulate (Chippindale and Milton, 1934; Miles, 1973). Where the sward has been established on land formerly under arable cultivation, large numbers of seeds of arable weeds may be found; these tend to occur at greater depths than those of species which have seeded after sward establishment, and their numbers decrease with the age of the grassland (Douglas, 1965). Meadows which are subject to seasonal flooding may receive appreciable quantities of seeds of arable and ruderal species which then become incorporated into the seed bank (Rabotnov, 1969; Mika, 1978).

From their examination of the seed banks of British grasslands, Champness and Morris (1948) concluded that "Many of the herbs of our grasslands may give a very high buried seed population and yet occur as no more than occasionals in the pasture". This appears to be generally true, although not all dicotyledons behave in this way. Seeds of some species which regenerate vigorously by vegetative means, such as *Cirsium arvense*, may be absent altogether or found only in low numbers. Another group of plants which can be recognized comprises short-lived species of which almost all the seeds produced in autumn germinate early in the following spring. Among them are Umbelliferae such as *Seseli libanotis* and *Pimpinella saxifraga* (Rabotnov, 1978; Thompson and Grime, 1979); seeds of species in this group would not be found in the buried seed bank.

The type of management of grassland would be expected to have an effect on the size and species composition of the seed bank, and

some studies have been made in which different regimes have been compared. Zelenchuk (1968) examined two grazed and two mown natural meadows in the L'vov region of the USSR and found that there were higher numbers of seeds under mowing. Few viable seeds of grasses and legumes occurred in the mown meadows, whereas with grazing they constituted more than 50% of the total. Golubeva (1962) observed no substantial difference in the seed banks of mown and unmown areas of meadow steppe, but in studies on peaty soils the seed numbers of grasses were less with mowing while those of *Carex* and *Juncus* spp. were greater (Zelenchuk, 1961). In Canada it was found that viable seeds of grasses were most numerous in ungrazed fields and lowest under heavy grazing, while the reverse was true for seeds of forbs and shrubs (Johnston *et al.*, 1969). Major and Pyott (1966) concluded from their own work on a California grassland and from other published studies that buried viable seed content is no indicator of grazing or mowing treatment. This is perhaps not surprising, since the differences in size and floristic composition of seed banks which develop under different management regimes will reflect the extent to which they favour or restrict growth and seed production of the range of species present in the vegetation.

The role of stock in relation to seed banks of grasslands has received some attention. The distribution of seeds in manure has been examined (Dore and Raymond, 1942; Boeker, 1959), and studies of the content of viable seeds in the surface soils of cattle resting places have been made in Germany (Boeker, 1959) and in Japan (Sugawara and Iizumi, 1964).

V. SEED BANKS OF AQUATIC ECOSYSTEMS

It was pointed out by van der Valk and Davis (1976) that except for the investigation of salt marshes by Milton (1939), the study of seed banks of wetland habitats has been almost completely neglected, although a knowledge of their floristic composition could lead to better understanding of successional patterns and also help in management. In a preliminary study, they determined the numbers of viable seeds present in different vegetation zones of eight prairie glacial marshes in Iowa. A major conclusion from this work was that there appeared to be very little floristic similarity in the seed banks from different marshes, even when the vegetation types sampled were the same. Those of different vegetation types within the same marsh, however, were more similar; this is because seeds of nearly all aquatic and marsh plants float or are wind-dispersed, and so in time could reach all zones within

a marsh. They concluded that the type of vegetation present at any one time depends mainly on the water level, but that its floristic composition reflects that of the seed bank.

In a later detailed investigation of two Iowa marshes (van der Valk and Davis, 1978), the numbers of viable seeds (including turions) found beneath different vegetation types ranged from 21 440 to 42 620 in 0–5 cm. The species contributing to the seed banks were of three kinds: emersed species with seeds which germinate on exposed mud flats or in very shallow water; submersed and free-floating species whose dormant seeds or turions can survive on exposed mud flats for a year and then germinate when there is standing water; ephemeral species whose seeds only germinate on the mud flats when there is no standing water. Primarily because of the fluctuations in water level and the effects of muskrat damage, cyclic changes take place in the vegetation of prairie marshes and the seed bank is the key to understanding their vegetation dynamics and survival (Fig. 2).

The possibility of reconstructing the recent vegetational history of

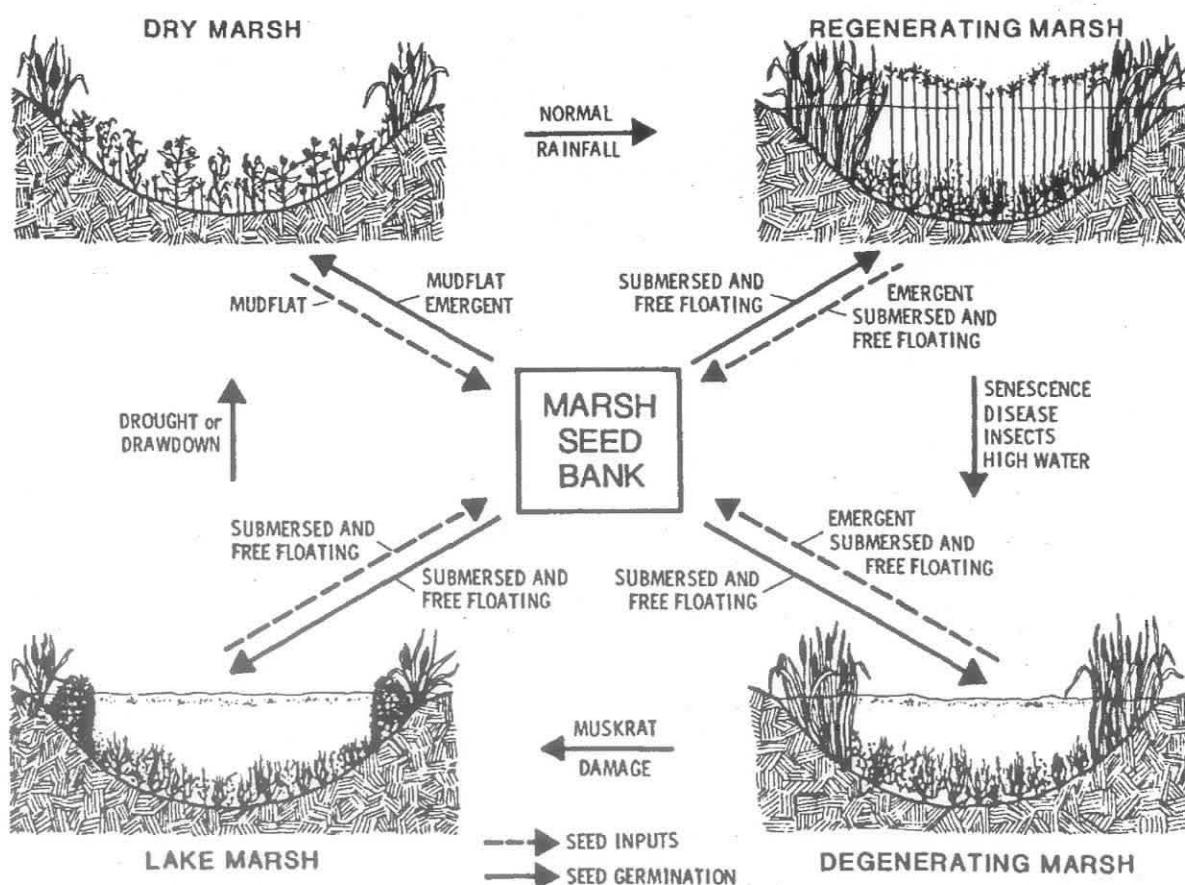


FIG. 2. Schematic presentation of the vegetation cycle and inputs and outputs of seeds from the seed bank during this cycle in a prairie glacial marsh in Iowa (from van der Valk and Davis, 1978; copyright 1978 by the Ecological Society of America).

a marsh from the seed bank was studied using soil samples from different depths in six vegetation types at Eagle Lake, Iowa (van der Valk and Davis, 1979). They concluded that this is possible to a greater or lesser extent, depending on the past and present communities, but that there are problems both of technique and interpretation. Some shallow-marsh vegetation types usually produce so few seeds that they cannot be detected, while others have dominant species whose seeds are difficult to germinate. Differential seed longevity must also be taken into account; seeds of mud-flat annuals and some emergent aquatics appeared to be long-lived, but those of many other aquatics remain viable for shorter periods.

Appreciable numbers of viable seeds were found in soils beneath several vegetation types of a fresh-water tidal marsh in New Jersey (Leck and Graveline, 1979), with mean values of 6400 to 32400 m⁻² in 0–10 cm. Seven out of the ten species most frequently represented were annuals, and a striking feature was the correspondence between the floristic composition of the seed banks and that of the seedling populations observed. Comparison with published data for other ecosystems showed that in the tidal marsh there were relatively large numbers of seeds below the surface layer. Water movement may be partly responsible for the lower seed numbers near the surface, and the data suggest that viability of buried seeds in marsh soils may be prolonged.

Studies have been made of a very different aquatic habitat—the floating islands of Lake Rawa Pening in Central Java (Hayashi *et al.*, 1978). These islands are formed initially by massive growth of *Eichhornia crassipes* on the surface. Soil and peat rising upwards become trapped by the roots and provide a substrate for establishment of other species. Successional stages lead to a community dominated by the grasses *Leersia hexandra* and *Eragrostis amabilis*, which is then invaded by shrubs. Examination of soil samples taken from different successional stages showed the presence of large numbers of viable seeds, equivalent to 8780 to 12250 m⁻² in 0–10 cm. The floristic composition of the seed banks did not correspond with that of the vegetational stages from which the samples were derived. Seeds of *Cyperus* spp. were abundant in soil from all the stages and also occurred in samples taken from the lake bottom. If the vegetation of the islands were to be destroyed, therefore, regeneration would occur from the seed reserves present.

Two studies of European marshland soils have recently been reported. Hunyadi and Pathy (1976) examined the seed banks of several marshes in western Hungary. Although high numbers of seeds of *Bulboschoenus maritimus* were found in some of them, the greatest numbers

were those of annual weeds common in adjacent arable areas, such as *Echinochloa crus-galli*, *Amaranthus retroflexus* and *Stellaria media*. Mika (1978) studied the seed banks of peat bog soils under permanent grass in South Bohemia where the dominant species was *Carex davalliana*. Numbers of seeds ranged from 1500 to 9200 m⁻² in 0–10 cm, and the floristic composition differed from that of the sward. The greatest numbers of seeds were of arable weeds, and their presence was apparently associated with water and insect distribution but not with wind dispersal. Except for some seeds of *Festuca rubra*, cultivated grasses were not represented; seeds of weedy grasses totalled 180–240 m⁻² and those of legumes 40–360 m⁻².

The considerable populations of viable seeds which accumulate in marshy areas in northern and western Europe dominated by *Juncus* spp. have already been mentioned. In contrast, Moore and Wein (1977) were unable to find any viable seeds in a *Sphagnum* bog community in New Brunswick with *Kalmia angustifolia*, *Ledum groenlandicum* and *Rhododendron canadense*, and only 320 m⁻² in 0–10 cm in a bog with *Larix laricina*.

VI. SEED BANKS OF FORESTS AND WOODLANDS

Studies of the litter and surface soil in North American forests have demonstrated the presence of viable seeds of species not represented in the vegetation and have indicated long-term survival of seeds of some species of previous successional stages (Oosting and Humphreys, 1940; Olmsted and Curtis, 1947; Livingston and Allessio, 1968). The numbers of viable seeds in the forest soils, especially in the oldest stands, were low compared with those of other vegetation types. Several other studies have since been made of the seed banks of different forest types in North America (Table VI).

A consistent feature of the coniferous forests examined was the absence of viable seeds of the dominant tree species, attributable to low seed inputs and rapid loss from the surface seed bank (Kellman, 1974a; Whipple, 1978). The total numbers of viable seeds present were low compared with those in other communities and in the series of stands examined by Moore and Wein (1977) were lower than those in deciduous-dominated forest. The values quoted in Table VI for Oregon (Strickler and Edgerton, 1976) include spores of the fern *Cystopteris fragilis* which gave rise to plantlets; if these are excluded, values ranging from approximately 300–1000 seeds m⁻² are obtained. The highest numbers were in the litter layer and most were of species such as *Epilobium watsonii* which produce abundant wind-borne seeds,

TABLE VI. Numbers of viable seeds in North American forest soils

Location	Forest dominants	Age (years)	Depth (cm)	Seeds (m ⁻²)	Authors
British Columbia	<i>Tsuga heterophylla</i>	100	0-10	1016	Kellman (1970)
	<i>Pseudotsuga menziesii</i>				
British Columbia	<i>Thuja plicata</i>	103	0-10	206	Kellman (1974a)
	<i>Tsuga heterophylla</i>				
Northwest Territories	<i>Pseudotsuga menziesii</i>				
	<i>Picea mariana</i>	180	0-10	0	Johnson (1975)
	<i>Picea glauca</i>	100	0-10	0	
	<i>Pinus banksiana</i>	100	0-10	0	
New Brunswick	<i>Betula papyrifera</i>	40+	0-12	3400	Moore and Wein (1977)
	<i>Fagus grandiflora</i>				
	<i>Acer rubrum</i>	40+	0-12	1950	
	<i>Fagus grandiflora</i>				
	<i>Acer rubrum</i>	40+	0-16	1230	
	<i>Abies balsamea</i>				
	<i>Picea mariana</i>	40+	0-14	580	
	<i>Pinus strobus</i>				
	<i>Pinus mariana</i>	40+	0-16	370	
	<i>Populus tremuloides</i>	c.40	0-10	399	Archibald (1979)
Saskatchewan	<i>Picea glauca</i>				
	<i>Betula papyrifera</i>				
	<i>Abies grandis</i>	130	litter + 4	421	Strickler and Edgerton (1976)
	<i>Pinus contorta</i>				
	<i>Abies grandis</i>	150	litter + 4	1863	
	<i>Picea engelmannii</i>				
Oregon	<i>Larix occidentalis</i>				
	<i>Abies grandis</i>	175	litter + 4	3447	
	<i>Subalpine, mesic</i>	325	0-5	53	Whipple (1978)
	<i>Picea engelmannii</i>				
	<i>Abies lasiocarpa</i>				
Colorado	<i>Subalpine, dry</i>	325	0-5	3	
	<i>Pinus contorta</i>				

although the soil beneath contained some viable seeds which had probably been present for long periods. Kellman (1974a) compared the seed banks of a forest and the secondary community arising after clear-felling. The two were comparable in floristic diversity, but whereas the forest included both primary and secondary species, the appreciably larger seed bank of the secondary community was made up mainly of *Senecio sylvaticus* and other species reproducing locally.

Subalpine forest in Colorado yielded very low numbers of viable seeds (Whipple, 1978). With a single exception at each of the two sites examined, the tree and understory species present in the forest were not represented in the seed bank. Very low numbers of seeds were also recorded from subarctic forest stands of varying ages (Johnson, 1975). In some of them no viable seeds at all were found (Table VI); in others there were no germinable seeds but small numbers of those extracted, of *Empetrum nigrum* and *Betula* spp. in particular, proved to be viable when subjected to tetrazolium tests.

The occurrence of viable tree seeds in five northern hardwood stands in Pennsylvania dominated by *Prunus serotina* with *Acer saccharum* and/or *A. rubrum* was studied by Marquis (1975). In spring, when the previous season's seedfall was still present, the average number was 370 m^{-2} , mainly *Prunus pensylvanica*, *P. serotina* and *Betula* spp. Three groups of species could be distinguished. Seeds of some species germinated mainly in the first spring (*Acer saccharum*, *Tsuga canadensis*, *Fagus grandiflora*), others had some seeds which regularly survived for 2–5 years (e.g., *Fraxinus americanus*, *Prunus serotina*, *Betula* spp.), while high numbers of *Prunus pensylvanica* seeds remained viable for 30 years or more after this species had died out of the overstory. A detailed study of *P. pensylvanica*, a successional species appearing after disturbance of northern hardwood forests, was made by Marks (1974). He demonstrated the presence of appreciable populations of viable seeds of this species in forest soils well after it had disappeared from the vegetation, and discussed the "buried seed strategy" in relation to disturbance and the stability of the forest ecosystem. Evidence for long-term seed survival in a few other species has also been obtained. Gratkowski (1964) found 37 viable seeds m^{-2} of *Ceanothus velutinus* var. *laevigatus* in the soil of old *Pseudotsuga menziesii* forest, with none in the litter or duff layers and no plants present. Del Tredici (1977) concluded that seeds of *Comptonia peregrina* could persist for 70 years or more beneath *Pinus strobus* forest in Connecticut.

In the USSR, a study of a 100-year-old southern taiga (*Picea abies*/*Vaccinium myrtillus*) forest revealed numbers of viable seeds ranging from 1200–5000 m^{-2} (Karpov, 1960). There was little correspondence between the floristic composition of the ground flora and that of the seed bank, and the species represented as seeds were largely those of early successional stages or of clearings. Similar results were reported by Petrov (1977) from a study of five forest types in the Moscow region in which the seedlings emerging on cleared plots were recorded. In old, comparatively undisturbed *Picea* or *Picea/Pinus* forests, seeds were present of herbs and shrubs which were absent or almost absent from

the vegetation; those of *Carex pallescens* and *Luzula* sp. were especially numerous. Although seeds of a few forest species such as *Oxalis acetosella*, *Ajuga reptans* and *Moehringia trinervia* were found in significant numbers, there were few or none of most of the characteristic ground-layer species. If felling took place, these species could not regenerate from seeds in the soil and most of the seedlings would be those of non-forest species. In secondary *Betula* and *Populus tremuloides* woodlands 20–30 or 30–40 years old, the numbers of viable seeds were about three times those of the primary forest and the range of species was greater.

In a 45-year-old *Picea abies* forest in the Belgian Ardennes there were more than 21 000 viable seeds m^{-2} in the 2–5 cm layer (Vanesse, 1976). The highest numbers were those of *Calluna vulgaris* and the seed bank provided a partial representation of the flora prior to afforestation. A study of cleared woodlands in Romania (Simtea, 1971) showed that the numbers of seeds decreased from the *Quercus* zone (300 m) through the *Fagus* zone (1000 m) to *Picea* (1400 m). There was a direct relationship between the extent of the seed bank and the degree of vegetation cover two years after clearing.

Only two studies appear to have been made of the seed banks of British woodlands. Thompson and Grime (1979) determined the germinable seeds present in the surface soil of a semi-natural wood in northern England dominated by *Quercus petraea* and noted a remarkable lack of correspondence between the vegetation and the seeds present. No seeds were found of some of the most frequent species in the ground flora, whereas of the five species with the highest seed numbers *Juncus effusus* was not recorded in the vegetation at all and *Digitalis purpurea*, *Milium effusum* and *Poa annua* were all infrequent. A detailed study of five coppice woods in southeast England which had been neglected for about 30 years was made by Brown and Oosterhuis (1981). They found an average of 1840 viable seeds m^{-2} in 0–5 cm, with *Juncus effusus*, *Betula* spp. and *Rubus fruticosus* the most frequent. Soil samples from the 5–15 cm layer revealed seed numbers which were on average only 20% lower than those from 0–5 cm. Of the species present in the vegetation of the densely shaded areas from which the samples were taken, only *R. fruticosus* was represented in the seed bank. Most of the seeds found were those of species which are light-demanding or which will tolerate only partial shade, and which occupy the ground immediately after coppicing. They concluded that most of the seeds had been present since the last coppicing, and that the seed bank plays a major part in floristic recovery.

Data on the seed banks of coniferous woodlands in Japan were obtained in studies of a series of stages in a secondary succession

(Numata *et al.*, 1964; Hayashi and Numata, 1964, 1968). As found in investigations of North American old-field successions, seeds of species of earlier stages were present and the dominant tree species were poorly represented in the seed bank. There was a progressive decrease in seed numbers from a young stand of *Pinus thunbergii* through mature *P. thunbergii* and overmature *P. densiflora* to climax *Shiia sieboldii*. Another investigation was reported by Nakagoshi and Suzuki (1977) who examined the viable seeds beneath seven forest types, mainly with *Pinus densiflora* as the dominant species, on Miyajima Island in southwestern Japan. They were particularly concerned to establish the floristic correlation between the vegetation and the seed bank and they divided the species into four groups. The first comprised "differential" species which were present in some communities but not others, usually both in the vegetation and the seed bank. The second included the main species present in the stands; the highest seed numbers were those of *Pieris japonica* with a mean of 320 m^{-2} in 0–10 cm, followed by *Cleyera japonica* (80 m^{-2}), *Ilex peduncularis* (33 m^{-2}) and *Pinus densiflora* (32 m^{-2}). The species in this group are important in maintaining the communities. The third group comprised species of which seeds were found but which were not present in the vegetation; they were mainly endozoochores, and may be pioneers when the forest is destroyed by fire or felling. The final group was made up of species present in the forest vegetation but not detected in the seed banks.

Some data are available on seed banks beneath Australian woodlands. A study of viable seeds in the soil of different woodland and scrub communities in Victoria revealed a range from 670 m^{-2} in 0–10 cm for *Leptospermum myrsinoides* heath to 35840 m^{-2} for savanna woodland (Carroll and Ashton, 1965). Seeds of dominant trees, such as *Nothofagus cunninghamii* and *Eucalyptus* spp., were few and most of the seeds found were those of herbaceous species. Similar results were obtained for a subalpine woodland dominated by *Eucalyptus pauciflora* var. *alpina* in Victoria (Howard and Ashton, 1967). The dominant species and several others common in the forest stand were not represented in the seed bank, which included many herbaceous species absent from the vegetation. Of the $1820 \text{ viable seeds m}^{-2}$ in 0–18 cm, 83% were in the top 2·5 cm. Howard (1974) examined the seed bank beneath closed *Nothofagus cunninghamii* forest, grassland dominated by *Poa gunnii* and an ecotonal stage with a tree stratum of *Acacia melanoxylon* in Tasmania. Few seeds of *N. cunninghamii* were found, but those of *A. melanoxylon* occurred in the forest soil even though this species was not present in the forest vegetation. The total bank of viable seeds was least in the forest soil and herbaceous species were the main

contributors, although largely absent from the vegetation. Howard and Smith (1979) studied the viable seeds beneath some forest and scrub communities in part of Sydney Harbour National Park. Significant numbers of seeds of weedy species were found even in apparently undisturbed vegetation, and would have to be taken into account in the management of the area.

The limited investigations of seed banks beneath tropical forests indicate the prevalence of seeds of species characteristic of secondary successions. Samples from mature forest in Nigeria (Keay, 1960) revealed seeds of only two economic timber trees. Most of the tree seeds recorded were those of typical forest regrowth species not present in the vegetation, while those of climbers, shrubs and herbs were also present. An examination of viable seeds beneath virgin forest in Sabah, Malaysia showed that 62% of those present were of secondary species (Liew, 1973). Guevara and Gómez-Pompa (1972) studied the viable seeds in soil beneath primary lowland tropical selva in Mexico and concluded that secondary species were the most important floristic element. Repeated sampling showed that seeds of some species were present throughout the year, indicating that dormancy is an important factor; no primary species showed this characteristic. They concluded that primary forest would not be restored if all trees in adjacent areas were destroyed, and that the seed bank is important in determining the direction of succession. In secondary vegetation of recent origin, the numbers of viable seeds were considerably higher than those beneath primary forest.

The results of these investigations indicate that most of the shade-tolerant true forest species do not produce seeds which enter the buried seed bank. This is also generally true for the dominant trees of mature forest. The greatest numbers of seeds found in soil beneath closed forest or woodland are those of species characteristic of more open habitats such as clearings or the early stages of secondary successions. In secondary forests seeds of these species which have become incorporated into the soil may persist in quantity for long periods, perhaps 40 years or more. The presence of seeds of secondary species in primary forest, however, suggests that immigration must occur. Kellman (1974a) showed that small quantities of seeds of secondary species were able to infiltrate for considerable distances, while Nakagoshi and Suzuki (1977) considered that bird dispersal was an important factor in the forest communities which they examined.

VII. SOME GENERAL CONSIDERATIONS

The investigations which have been reported lead to the conclusion that the presence of appreciable reserves of viable seeds in the soil is a feature of a wide range of plant communities. The main exceptions appear to be mature temperate and tropical forests, where seed banks tend to be replaced by banks of persistent seedlings (Grime, 1979). The very limited evidence also suggests that seed numbers are likely to be low in the vegetation of arctic regions. Johnson (1975) found scarcely any viable seeds in the soil of subarctic forests, and concluded that there is a trend towards a decline in the size of the seed bank with increasing latitude.

As Thompson (1978) has pointed out, there are also general tendencies for the size of the seed bank to decline with increasing altitude and in the later stages of plant successions. He suggests that this variation, both on a local and on a continental scale, might be accounted for in terms of disturbance (anything which causes the destruction of all or part of the vegetation) and stress (mechanisms limiting the rate of production of biomass of all or part of the vegetation). A decline in seed numbers would be expected with decreasing intensity of disturbance and with increasing levels of stress, and evidence to support this is adduced from published studies of the seed banks of British grasslands and of North American herbaceous and forest vegetation. He concludes that the existing data fit reasonably well into an explanatory scheme based on gradients of stress and disturbance, but that more data are needed to test the hypothesis.

The species composition of a seed bank reflects the differing strategies of past and present components of the vegetation, and great diversity is apparent. At one extreme are species which produce large numbers of seeds, many of which are capable of remaining viable for long periods when buried; these are often the major contributors to seed banks. At the other are species in which regeneration is entirely or mainly clonal, or that produce seeds which all germinate rapidly, retain viability for only a short period, or are subject to severe predation. These species either do not occur in seed banks or are represented for only a limited part of the year by seeds present at or near the soil surface.

A useful classification (Fig. 3) which is applicable to individual species has been proposed by Thompson and Grime (1979) on the basis of a study of seed banks in a range of habitats. The main distinction is drawn between transient seed banks (Types I and II) in which no viable seeds remain for longer than a year, and persistent seed banks

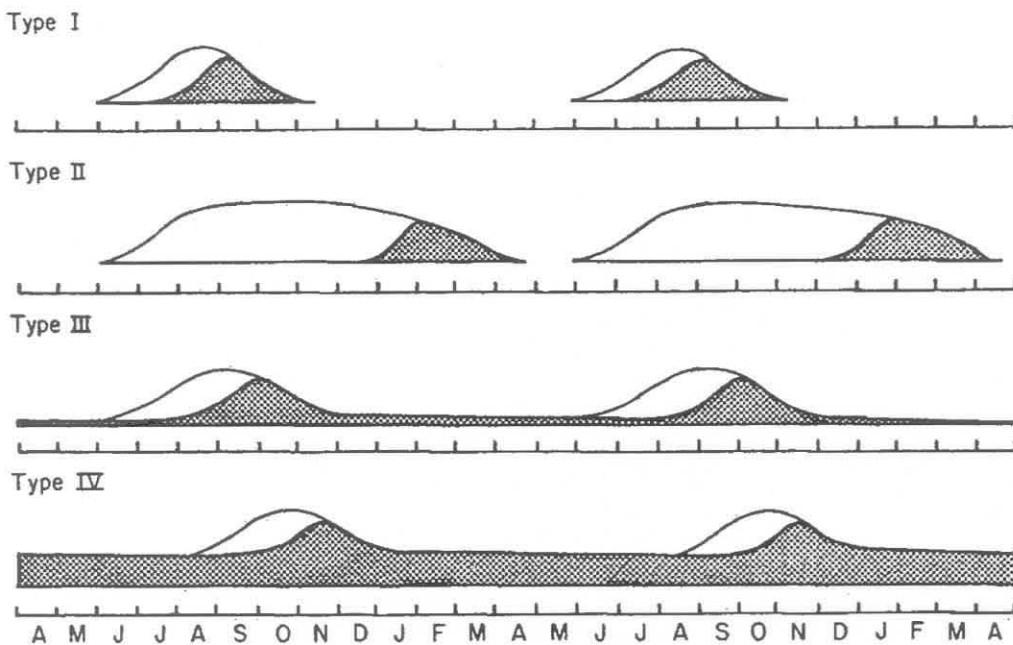


FIG. 3. Diagrammatic representation of four types of seed bank. Shaded areas: seeds capable of germinating immediately after removal to suitable laboratory conditions. Unshaded areas: seeds viable but not capable of immediate germination. Type I: annual and perennial grasses of dry or disturbed habitats. Type II: annual and perennial herbs colonizing vegetation gaps in early spring. Type III: species mainly germinating in the autumn but maintaining a small persistent seed bank. Type IV: annual and perennial herbs and shrubs with large persistent seed banks (from Thompson and Grime, 1979).

(Types III and IV) in which there is a carry-over of some viable seeds from year to year. The species which form transient seed banks are adapted to exploit the gaps created by seasonally-predictable damage and mortality in the vegetation, while the persistent seed bank (Type IV) confers the potential for regeneration in circumstances where disturbance of the vegetation is temporally and/or spatially unpredictable. Species with Type III seed banks show intermediate characteristics. The functional significance of the different types and the relationships with the seed morphology and germination physiology of the species concerned are discussed by Grime (1979) and Thompson and Grime (1979). In each of the ten plant communities which Thompson and Grime examined there were some species which had persistent seed banks, and there were usually others of which viable seeds were present for only part of the year.

The question of the fate of seeds while at the soil surface and after they have become part of the buried seed bank has been considered

by Sagar and Mortimer (1976), who presented life tables for some of the few plant species in which the gains and losses from the seed bank have been quantified. Recent studies have provided further data for particular species and communities (e.g. Keeley, 1977; Nelson and Chew, 1977; Watkinson, 1978; Turkington *et al.*, 1979). One investigation of particular interest is that by van der Vichte (1978) of the population dynamics of *Stellaria media* on a sandy soil in the Netherlands. He found that there were two distinct populations, with the plants growing side by side, which differed in life-cycle strategy. In one of them almost all the seeds germinated in autumn and the seed bank was replaced annually; in the other, there was a persistent and phenotypically diverse seed reserve. As he points out, it seems a reasonable assumption that population differences of this kind will be detected in other species if more attention is paid to individual plants.

One aspect which is of particular significance in relation to the species which form persistent seed banks is the pattern of loss of viable seeds from the reserves and the way in which this may vary under different conditions. As already mentioned, there is evidence that in soil subjected to a consistent regime of disturbance the numbers of viable seeds of many arable weeds decrease exponentially from year to year (Roberts, 1962; Roberts and Dawkins, 1967). Further data have been obtained from experiments in which seeds have been mixed with soil and the numbers of viable seeds or of emerging seedlings recorded during successive years (Roberts, 1964; Roberts and Feast, 1973a; Watanabe and Hirokawa, 1975).

TABLE VII. Seedling emergence in successive years and survival of seeds freshly harvested in late summer or autumn, mixed with 7.5 cm of soil and cultivated three times per year. Means of three experiments begun in different years

Species	Seedlings emerged as % of seeds sown						Viable seeds remaining as % of seeds sown
	Initial ¹	Year ²	Year	Year	Year	Year	
			1	2	3	4	5
<i>Hordeum murinum</i>	87.8	0	0	0	0	0	0
<i>Anthriscus sylvestris</i>	0	77.3	1.2	0	0	0	0
<i>Lamium amplexicaule</i>	19.4	43.2	8.0	2.2	0.5	0.2	4.6
<i>Rumex crispus</i>	3.0	37.8	15.0	6.1	2.0	0.6	7.5
<i>Atriplex patula</i>	0	5.6	12.3	9.7	4.7	3.9	14.2
<i>Aethusa cynapium</i>	0	4.6	10.0	12.4	10.8	6.2	21.0

¹The period from sowing until 31 December.

²Calendar years.

Some results from experiments of this kind are summarized in Table VII. Those for *Hordeum murinum* and *Anthriscus sylvestris* are representative of species with transient seed banks, germination occurring either in autumn soon after sowing (Type I of Thompson and Grime, 1979) or in early spring (Type II), with few if any viable seeds remaining after that. The other four species form persistent seed banks (Types III and IV). For *Lamium amplexicaule* and *Rumex crispus* the decrease in seedling numbers was approximately exponential once the initial emergence had taken place. In *Atriplex patula* maximum emergence did not occur until the second year, and in *Aethusa cynapium* not until the third; this appears to be a result of innate dormancy imposed by the seed coat. The depletion of the seed bank is most rapid when the seeds are present in a shallow layer of soil and when there is frequent disturbance (Roberts and Feast, 1972, 1973a); under these conditions the role of enforced dormancy is minimized.

The scheme proposed by Thompson and Grime (1979) and shown in Fig. 3 takes account of the presence of innate dormancy, but implies that once this has been overcome the seeds will germinate if transferred to suitable conditions. This may well be true, but there is evidence for some species that changes in the dormancy status of buried seeds can occur as a result of the temperature conditions which the seeds experience. Induced dormancy may develop which then requires a period of exposure to temperatures within a particular range before germination can take place. In these species, therefore, seeds held under enforced dormancy undergo cyclic physiological changes in response to seasonal temperature variations. These not only serve to regulate the time of year at which emergence of seedlings can occur (Montegut, 1975), but may well increase longevity since germination is possible during only part of the year (Fig. 4). The general question of dormancy in relation to seed survival in the soil has been discussed by Roberts (1972).

The pattern of decline for persistent seed banks in undisturbed surface soil also appears to be exponential (Roberts and Dawkins, 1967; Roberts and Feast, 1973a; Watanabe and Hirokawa, 1975), and the data of Forbes (1963) and Thurston (1966) for survival of seeds of *Avena fatua* and *A. ludoviciana* under leys also conform to this pattern. There are few other studies in which seed survival under natural conditions has been determined for long enough to characterize the form of the decline curve. Bowes and Thomas (1978) constructed a curve for seed survival of *Euphorbia esula* in 0–2·5 cm, using data from different sites, which showed a linear rather than an exponential decrease of 13% per year over an 8-year period.

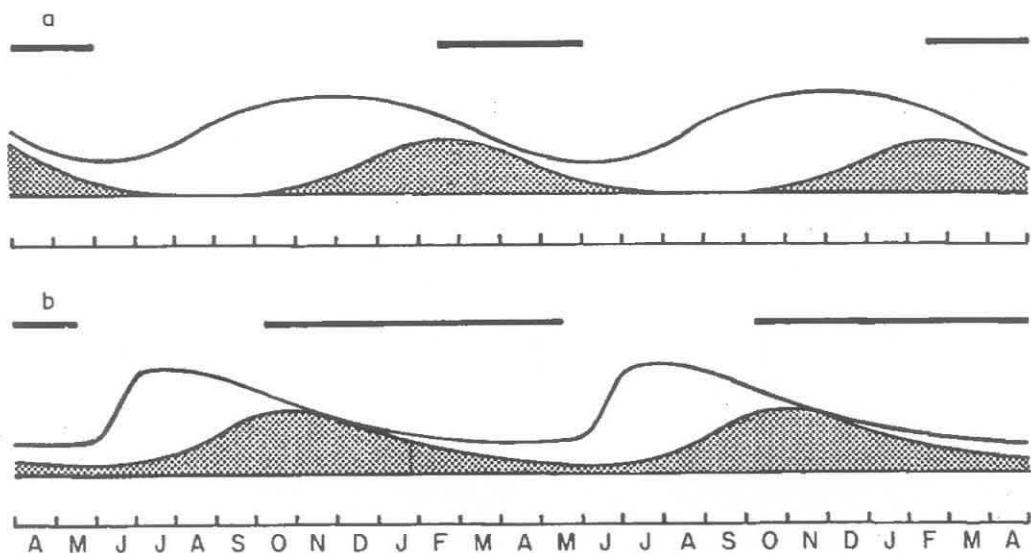


FIG. 4. Diagrammatic representation of persistent seed banks of two species of arable weeds. Shaded areas: seeds capable of germinating immediately after removal to suitable laboratory conditions. Unshaded areas: seeds viable but not capable of immediate germination. Horizontal bars: period of seedling emergence in the field. a: *Polygonum aviculare* (data of Courtney, 1968). Innate and induced dormancy overcome by low temperatures; induced dormancy re-imposed in late spring. b: *Veronica hederifolia* (data of Roberts and Lockett, 1978). Innate and induced dormancy overcome by high temperatures; induced dormancy re-imposed during winter and spring.

Seeds distributed in soil layers close to the surface are subject to predation and to wide fluctuations in temperature and moisture. These factors combined with inherent variability in the seed population, especially when seeds of different ages are involved, are presumably responsible for the exponential decline observed in species with persistent seed banks. The situation is different for seeds which are buried at depth, where conditions are much more uniform (Harper, 1957). Here it is probable that external factors are relatively less important and longevity depends much more on the inherent properties of the seed. Certain species appear to be particularly well able to survive in this situation; *Hyoscyamus niger* and *Verbascum thapsus* are two species for which there is good evidence of long-term seed survival in undisturbed sites (Ødum, 1978). In the Duvel experiment (Toole and Brown, 1946), seeds of *Solanum nigrum* buried at depths of 20 cm or more had approximately 80% viability after 39 years. In contrast, a naturally-occurring population of seeds of this species distributed in 0–23 cm of undisturbed soil declined exponentially at a rate equivalent to a loss of about 23% per year (Roberts and Dawkins, 1967).

In experiments in which seeds are buried at depth one might expect some initial loss, varying very much with species and with the time

of year at which the experiment is begun, because of germination before dormancy is enforced. There might then be a period of little change in the numbers of viable seeds remaining, with finally a fall to zero as the seeds die. Data obtained by Burnside *et al.* (1977) for seeds of *Sorghum bicolor* buried at a depth of 22 cm show these three phases very clearly. There was an initial loss of about 60% of the seeds in the first year, little change in numbers for the next seven years, and then a gradual decrease in the final five years of the experiment, reflecting the variability within the seed sample.

In respect of a persistent, buried seed bank three situations can thus be recognized. In soil which is periodically disturbed, dormancy will be enforced for only part of the time and mechanisms of innate and induced dormancy will play a large part in determining persistence. Where the seeds are distributed in undisturbed soil fairly close to the soil surface, perhaps to a depth of 20 cm or so, the role of enforced dormancy becomes more important. Finally, in seeds buried at depth under comparatively uniform conditions the intrinsic capacity for survival in the imbibed state becomes dominant.

VIII. CONCLUDING REMARKS

The presence of viable seeds in the soil is clearly relevant to the study of plant communities: as Major and Pyott (1966) observed "plants occurring in this form are part of the flora, which helps to determine the community, even though they are not readily evident". In the past ecologists have tended to ignore the seed bank, perhaps partly deterred by the difficulties in assessing it. Recently, however, there has been an upsurge of interest in seed banks, related to developments in the study of life-cycle strategies of plant species, plant demography and vegetation dynamics (Sagar and Mortimer, 1976; Harper, 1977; Rabotnov, 1978; Grime, 1979; Miles, 1979; Thompson and Grime, 1979).

From the practical point of view the viable seeds in the soil may be regarded as posing problems or as conferring benefits, depending on the situation. In arable cultivation, the presence of usually large numbers of seeds means that there is a continuing need for weed control; here the objective is to maintain the seed bank at the lowest feasible level in order to minimize interference with crop production. As already mentioned, the advent of selective chemical methods of weed control for most crops has enabled this to be achieved more readily than before. Repeated use of particular herbicides, however, by allowing seed production in some species and not others can markedly alter the

composition of the seed bank and hence that of the weed vegetation appearing in future crops. The increasing incidence of selection of biotypes resistant to herbicides, particularly the *s*-triazines (Strykers, 1979), is especially significant in this respect. The period for which viable seeds remain in the soil is one of the factors determining when resistance is likely to appear (Gressel, 1978).

Seed bank studies can make a contribution to improving the efficiency of crop production in various ways. A knowledge of the extent to which viable seeds are likely to persist in the soil has obvious relevance in assessing the consequences of changes in cropping and cultivations. Quantitative studies of the fate of seeds of weed species under different conditions (Wilson and Cussans, 1975; Mortimer, 1979) are particularly important in providing a basis for sound advice on control measures. Although viable seeds of crop species normally form only a small proportion of the total seed bank of arable soils, their persistence can be troublesome. Crops with which problems can arise include cereals, where disease carry-over is a prime concern (Hughes, 1974), and sugar beet, in which the annual bolting types can persist from crop to crop as seeds in the soil (Longden, 1974). The persistence of potato seeds is also being examined (Lawson and Wiseman, 1979).

The use of seed-bank data in monitoring the success of long-term weed control programmes is an aspect which could attract greater attention as the concept of weed management gains wider recognition; species which regenerate mainly or entirely by vegetative means would, of course, require separate consideration. Altieri and Whitcomb (1979) have suggested that the weed flora might be manipulated, by soil disturbance at particular times of year, to encourage those species whose presence can greatly increase the populations of beneficial insects. Knowledge of the species composition of arable seed banks can be used predictively in a general way to give guidance on the choice of herbicides (Dechkov, 1978), but how far relationships between seed numbers and seedling densities can be quantified and used for short-term forecasting of weed floras remains problematical. For this, and indeed for other purposes, techniques of estimation of viable seeds more rapid than those at present available would be desirable; however, the prospects for improvement do not seem very hopeful.

In grasslands, persistent seed banks of the less-desirable grasses contribute to sward deterioration and can pose problems when it is renewed. At the same time reserves of seeds of leguminous species are valuable in the maintenance of pastures, especially in regions subject to drought. In forests and woodlands the presence of viable seeds is

a major factor determining the direction of succession after destruction of the trees by fire or felling.

In these and other communités, the seed bank has a role in maintaining floristic diversity and must be taken into account in management. Baskin and Baskin (1978) cite results which demonstrate the function of a persistent seed bank in enhancing the genetic diversity and stability of a plant population at a particular site, and point out that this is especially significant for narrowly endemic species which occur in small populations. The wider genetic implications of seed banks have been discussed by Levin and Wilson (1978). One direct use of the seed bank is in the restoration of disturbed land; Beauchamp *et al.* (1975) found that the soil at potential strip-mining sites in Wyoming contained sufficient seeds in 0–5 cm to revegetate the areas, although most were those of species of secondary successions. This aspect has been discussed by Johnson and Bradshaw (1979).

The main concern of this article has been to review recent work on seed banks in a range of vegetation types. The seed bank, however, is in a state of dynamic flux; seeds enter it and leave it, and while remaining in it undergo physiological changes which can affect their response to the present and future environment. There has been a trend from mainly descriptive studies of the occurrence of seeds in the soil to those in which attempts are made to quantify seed inputs and losses and to determine the mechanisms by which they are brought about. Continuation of these approaches will not only increase understanding of how plant communities are regulated but is likely also to bring practical benefits.

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